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Importance of reproductive biology of a harvest lizard, *Tupinambis merianae*, for the management of commercial harvesting

Sergio Naretto A,B, Gabriela Cardozo A, Cecilia S. Blengini A and Margarita Chiaraviglio A

Abstract

Context. Management of the exploitation of resources requires biological information on exploited species. The skins of large reptiles have a commercial value as luxury leather items and *Tupinambis* lizards from southern South America have historically been exploited for this purpose. Argentina implemented management plans for *Tupinambis* lizards since 1988 that established a minimum capture size based on the width of dried skins, but this prescription has not been linked to local reproductive attributes of species.

Aim. In this study, we aim to determine the reproductive parameters of *Tupinambis merianae* and evaluate which class sizes of individuals are susceptible to commercial trade in central Argentina to generate local and species-specific information to improve available management tools.

Methods. We determined the relationship between the width of dried skins and live body sizes. We identified size at sexual maturity in males and females. Moreover, we determined status of reproductive individuals by body size and characterised gonadal development and seasonal reproductive events in central Argentina. We evaluated the relationship between female body size and clutch size.

Key results. Reproduction of *T. merianae* in central Argentina is markedly seasonal, with both sexes concentrating their reproductive activities between October and December. Size at sexual maturity was smaller for males than females, and the percentage of reproductive females was lower than males. In both sexes, the frequency of reproductive individuals was low in smaller lizards, and bigger females had bigger clutch size. The width of dried skins was positively related to body size.

Conclusions. Size at sexual maturity, and reproductive period, should be taken into account when management plans are designed to minimise any negative impacts of harvesting.

Implications. In central Argentina, the breeding season coincides with hunting periods set by national legislation. The results of our study have prompted local authorities to impose hunting closures for part of December and to raise the minimum catch size. Further, we offer an equation that can be used as a monitoring tool for estimating snout to vent length of live animals from skins. Studies like ours should be replicated in different areas and extrapolated to other models.

Additional keywords: harvest, maturity size, seasonal reproduction, monitoring, skins.

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Introduction

Reptile populations are being seriously reduced throughout the world (Nobrega Alves and Pereira Filho 2007; Böhm et al. 2013). The collection of wild animals for subsistence or commercialisation has been invoked as a factor contributing to the declines seen in certain species (Gibbons et al. 2000). The skins of several species of large reptiles including *Tupinambis* lizards, which are the largest terrestrial lizards in South America, have a high commercial value because they can be used for luxury leather items. *T. merianae* and *T. rufescens*, in particular, have been commercially harvested for their skins since the middle of the last century, and are among the most exploited reptiles in the world (Norman 1987; Fitzgerald 1994;

Mieres and Fitzgerald 2006). *T. merianae* and *T. rufescens* were included on Appendix II of the Convention on International Trade of Endangered Species of Wild Fauna and Flora (CITES) before 1980. In Argentina, commercial harvest of these species is allowed (Porini 2006; Resolución N° 11/2011 http://www.senasa.gov.ar/contenido.php?to=n&in=1506&io=19543 and Res. N° 1564/2013 Secretaría de Ambiente y Desarrollo Sustentable de la Nación Argentina). Although these *Tupinambis* species are not categorised as threatened in Argentina (Vaira *et al.* 2012), the exploitation of resources and CITES requires biological information and monitoring for decision making to ensure sustainable development of the activity and species protection.

^ALaboratorio de Biología del Comportamiento, Facultad de Ciencias Exactas Físicas y Naturales, Universidad Nacional de Córdoba, Vélez Sársfield 299, Córdoba, Argentina. CP X5000JJC.

^BCorresponding author. Email: narettosergio@gmail.com

Tupinambis merianae occur in diverse regions of South America (Cei 1993; Lanfri et al. 2013). Species that occur over very large geographic areas are less vulnerable to extinction (Webb et al. 2002). However, species with large distributions are also likely to exhibit spatial variability in their biological traits (Kwiatkowski and Sullivan 2002; Du et al. 2005). The spatial heterogeneity of T. merianae habitats (Cardozo et al. 2012) means that conservation management must be context specific. The Province of Córdoba, in central Argentina, represents one of the southernmost areas of their distribution (Lanfri et al. 2013) and includes the Espinal and Pampas ecoregions, which are severely degraded, mainly due to crop farming (Zak et al. 2004; Brown et al. 2006; Zak and Cabido 2008). Anthropogenic degradation of habitats has reduced the ability of many animal species to withstand hunting pressure (Shine et al. 1998). Also, central Argentina lies at the limit of geographic distribution of T. merianae, where environmental conditions reflect dynamics of dispersal and extinction risk (Brown et al. 1996; Lanfri et al. 2013), and could influence reproductive parameters (Diaz et al. 2007). Thus, interpretation of local biological traits and extrapolation to monitoring in a given environmental context would seem essential to conserving harvested species. Characterising the reproductive attributes of exploited species may help to frame management plans that minimise the ecological impact of the trade (Shine et al. 1999) by identifying times, sexes and sizes where harvesting should not occur. These studies are important because monitoring systems for Tupinambis lizards should rely on site-specific datasets to contemplate geographic variation (Mieres and Fitzgerald 2006). They are also useful for replication in different areas and extrapolation to others' models.

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Monitoring large-bodied lizard populations is difficult. Squamate reptiles are extremely variable in their activity, making transect counts and mark-recapture studies inefficient (Rodda et al. 1999, 2001; Mieres and Fitzgerald 2006). Large numbers of Tupinambis skins accumulate at different levels of the commercial trade, and it should be feasible to obtain information from them (Getz and Haight 1989; Fitzgerald et al. 1991; Shine et al. 1996; Mieres and Fitzgerald 2006). Sex can be determined from skins; therefore, a great deal of information on population structure is potentially obtainable from harvest monitoring (Mieres and Fitzgerald 2006). Argentina implemented management plans for Tupinambis lizards, establishing a minimum capture size based on the width of dried skins (Porini 2006). This policy is aimed at prohibiting the sale of skins from subadults, allowing more of them to reach maturity and reproduce, which may result in a higher population growth rate (Fitzgerald 1994). This parameter is applied to all territories of Argentina and for both species of Tupinambis present there (T. merianae and T. rufescens). However, the size of a dried skin is not the same as the size measured from a live Tupinambis specimen (Mieres and Fitzgerald 2006), and hunters might restretch small skins to achieve larger sizes (Fitzgerald et al. 1991). Furthermore, this information from skins should be associated with the biological attributes of species, like reproductive parameters, because reproductive attributes of species are essential for population growth and sustainable development of the commercial activity

(Shine et al. 1999). Size at maturity is pivotal: life history traits can affect other key traits, such as annual and lifetime fecundity (Wapstra et al. 2001; Cardozo and Chiaraviglio 2011), and can differ across populations influenced by local environment (Rohr 1997). Seasonal reproduction is a common pattern in *T. merianae* but may change geographically due to bioclimatic conditions. Seasonal reproductive activity (gonadal development, egg presence, postures, etc.) may play an important role in making particular sizes and reproductive condition of *Tupinambis* more vulnerable to hunters at a given time. Another important factor is body size of females because this factor is positively correlated with fecundity for most lizards where clutch size is variable (Fitch 1970; Cox et al. 2003).

In the present study, we aim to improve management tools by determining reproductive parameters of *T. merianae* and evaluating which sizes of individuals are susceptible to commercial trade in the Pampa and Espinal regions. The objectives of the study are to: (1) determine the relationship between dried skin width and body size of *T. merianae*; (2) identify sexual size at maturity in males and females and proportions of reproductive individuals based on body size; (3) characterise gonadal development and seasonal reproductive events; (4) evaluate the relationship between female body size and clutch size, and (5) analyse the harvest from the monitoring data to determine the classes and sexes of lizards captured, and establish a baseline for future comparisons.

Materials and methods

Species and study area

Tupinambis merianae is a Teiidae lizard that, at adulthood, can exceed 50 cm snout to vent length, or SVL (130 cm total length), weigh up to 4.7 kg (Fitzgerald et al. 1991; Avila-Pires 1995; Andrade and Abe 1999; Naretto et al. 2014) and undergoes a great shift in body size during ontogeny. The species overwinters in burrows, emerges during the hot season and breeds seasonally (Mercolli and Yanosky 1990; Fitzgerald et al. 1991). Specimens used in this study were collected in central Argentina (30°55′S, 63°40′WS to 31°55′S, 62°15′W), corresponding to the Espinal and Pampa regions.

Data collection

Individuals were caught weekly from wild populations by rural people between October and March from 2008 to 2012 (Resolución Córdoba Nº 750/2009 http://www.boletinoficial. gov.ar/DisplayPdf.aspx?s=01&f=19971231, Res. N° 1399/2010 http://boletinoficial.cba.gov.ar/wp-content/4p96humuzp/2014/ 11/091210_seccion1.pdf, Res. N° 1179/2011 http://boletinoficial. cba.gov.ar/wp-content/4p96humuzp/2014/12/301211_seccion1. pdf and Res. N ° 865/2012 http://www.cba.gov.ar/wp-content/ 4p96humuzp/2014/08/Resolucion1288-12-Paicor.pdf). Hunters detect lizards by direct observation or with the help of dogs (at this stage, the hunters do not select individuals by size or sex). They then follow the lizards to their burrows, where they are dug out and captured alive (allowing for release of individuals that do not meet minimum size requirements). In our study, lizards were killed in accordance with AVMA Guidelines on Euthanasia (AVMA 2013). We are authorised by government environmental agencies for scientific studies. We conducted a measure and re-measure experiment to obtain a regression for estimating SVL of harvested *T. merianae* from dried skins. We marked 60 live individuals (30 females and 30 males) and measured their SVL. After they were killed, their skins were stretched and dried by the hunters. We measured skin width at the midpoint of the longitudinal section and used this to derive an equation for the relationship between SVL and skin width.

We recorded date, sex and SVL of *T. merianae* hunted from 2009 to 2012 (taking into account variability of bioclimatic factors in different seasons). The sex, reproductive condition and sexual maturity of the lizards were diagnosed by inspection of their reproductive organs. In females, we measured follicular diameter, and in males, we recorded testis mass (TM). Females were considered reproductive if they had oviducal eggs, enlarged vitellogenic follicles (>7 mm) or corpora lutea (Garcia Valdez et al. 2011; Cardozo et al. 2015). In males, we recorded the presence of sperm in the epididymis; samples of seminal fluid were examined under a phase contrast microscope (Nikon eclipse Ti; Nikon Instruments Inc., Tokyo). The SVLs of the smallest reproductive female and male were used to estimate potential size at sexual maturity (Madsen et al. 2006; Cardozo and Chiaraviglio 2011). We described gonadal development across season and identified reproductive events. We calculated the proportion of reproductive individuals in different body size classes during the reproductive season only (to avoid overestimating the proportion of non-reproductive individuals outside the reproductive period). We determined body size classes based on SVL, using intervals of 2.5 cm; 29.5–32 cm; 32–35.5 cm; 35.5–37 cm; 37–39.5 cm; 39.5–42 cm; 42-44.5 cm; and 44.5-47 cm. Clutch size was determined by counting egg postures and eggs in oviduct and corpora lutea.

Finally, we used skin monitoring data for the 2005-06 (n=6400) and 2006-07 (n=6300) hunting seasons, which occurred prior to our study (legal regulation of the activity did not change among these seasons). The monitoring data were collected and provided by the Córdoba wildlife agency (Secretaria de Ambiente del Ministerio de Agua, Ambiente y Servicios Públicos de la Provincia de Córdoba). Sex of lizard skins was determined based on the presence (in males only) of an enlarged scale in the cloacal region (Fitzgerald *et al.* 1991). We used the equation obtained in this study to estimate the SVL of lizards from dried skin widths in the monitoring sample.

Statistical analyses

Dried skin width was regressed on SVL. We tested for homogeneity of slopes among sexes with an ANCOVA sex by SVL (covariate) interaction term. To test differences in frequency distributions of body size classes with respect to reproductive condition and sex, we used the Chi-square test. Clutch size was regressed on female SVL. To illustrate temporal dynamic of gonads and reproductive events, we selected periods of 15 days. Statistical analyses were performed using INFOSTAT version 2012 (Universidad Nacional de Córdoba) and SPSS 16.0 (SPSS 16.0 Inc., Chicago, IL).

Results

We observed a positive relationship between SVL of live *T. merianae* specimens and the width of their dried skins

(Fig. 1) $(F_{1, 59} = 351.05, r = 0.81, P < 0.001)$. The slope of this relationship was similar for the sexes (ANCOVA: interaction term sex × covariate SVL $F_{1,56} = 0.541, P = 0.465$). The smallest reproductive male (with spermatozoa in the epididymis) had an SVL of 29.5 cm. The smallest reproductive female (with corpora lutea) had an SVL of 32 cm.

Gonadal development was seasonal in males and females. The greatest testis mass was observed in November (Fig. 2). We observed males with spermatozoa in their epididymis from October to January, with 97% (108 of 111) of these observations made between 15 October and 31 December (Fig. 2). Females with vitellogenic follicles occurred from 15 October to 31 December, with 85% (57 of 67) between 1 November and 15 December. We found females with eggs in their oviducts between 15 November and 15 December (21 females), and corpora lutea from 15 November, indicating the onset of ovipositioning (13 females) (Fig. 2). We observed egg laying from 20 November to 20 December. We observed two pairs copulating in the field, on 29 October and 15 November. The mean SVL of reproductive males (with sperm in epididymis) was 39.7 cm (range 29.5–49.0 cm, n = 110). The mean SVL of reproductive females was 38.4 cm (range 32-44 cm, n = 90).

Body size distribution differed among reproductive condition classes for both sexes (males: Chi square test: $\chi^2 = 15.03$; d.f. = 7; P = 0.028; females: Chi square test: $\chi^2 = 17.77$; d.f. = 5; P = 0.032) (Fig. 3). In total, 65% of males found during the breeding season had sperm in their epididymis (reproductive condition) and 50% of females were reproductive. Body size distribution of reproductive individuals differed between the sexes (Chi square test: $\chi^2 = 25.12$; d.f. = 7; P = 0.001). In males, reproductive condition was more frequent than non-reproductive condition in

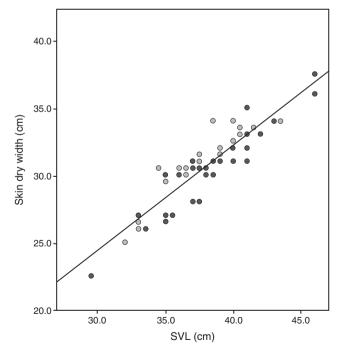


Fig. 1. Dried skin width in relation to SVL of *Tupinambis merianae* (black circle: males; grey circle: females). Least-squares regression lines are shown for *T. merianae* (both sexes): Dried Skin Width = 0.78 SVL + 1.007.

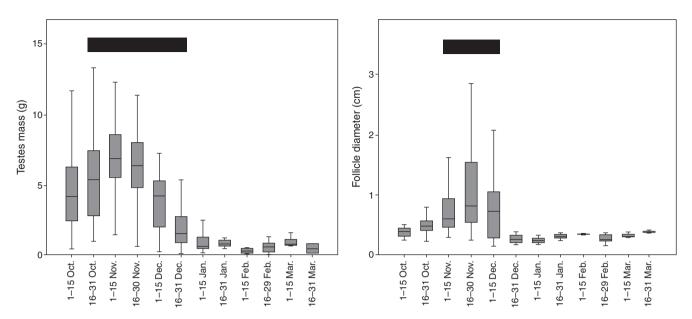


Fig. 2. Gonadal development across seasons. Horizontal black bars indicate the period of sperm presence for males and eggs in oviduct for females.

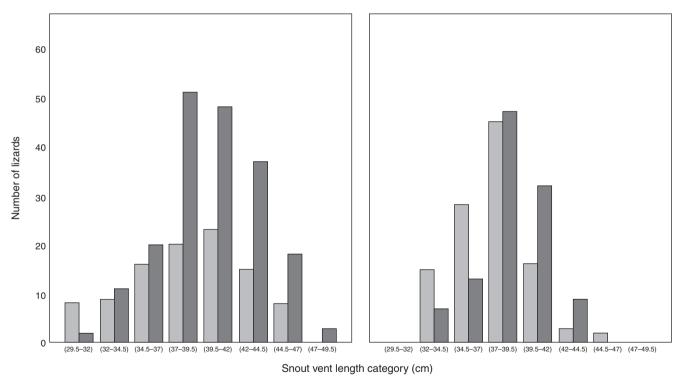


Fig. 3. Body size distributions of reproductive (black) and non-reproductive (grey) *Tupinambis merianae* during breeding season (October 15 to December 31). Left: males; right: females.

body size classes larger than 32.0 cm, and in females this was true for body size classes larger than 39.5 cm (Table 1).

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We observed a positive relationship between clutch size and maternal body size ($F_{1,22}$ =40.02, P=0.001, R^2 =0.63, n=24) (Fig. 4).

The sex ratio among skins in the monitored sample from 2005 to 2007 was 52% females and 48% males (5627 males and 6026 females). There were differences between the sexes in the body size distributions of monitored lizards (Chi square test: $\chi^2 = 922.95$; d.f. = 7; P = 0.001). More males than females

Table 1. Percentage of reproductive individuals of each sex by body size categories of live animals, and dried skin width for these categories

Snout-vent length estimates from SVL (cm) = (skin width (cm) - 1.007) / 0.78.

SVL (cm)	Dried skin width (cm)	Percentage of males in class that are reproductive (%)	Percentage of females in class that are reproductive (%)
29.5–32.0	24.0–26.0	20	_
32.0-34.5	26.0-28.0	55	32
34.5-37.0	28.0-29.9	55	32
37.0-39.5	29.9-31.8	72	51
39.5-42.0	31.8-33.8	68	66
42.0-44.5	33.8-35.7	71	75
44.5-47.0	35.7–37.7	69	_
47.0-49.5	37.7–39.6	100	_

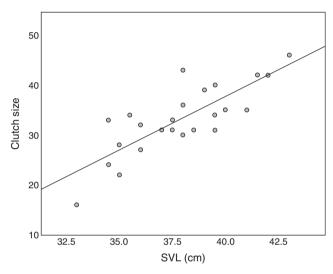


Fig. 4. Relationship between clutch size and maternal body size.

of larger body size classes were captured (Fig. 5). Of captured females, 29% were in body size classes less than 37 cm SVL.

Discussion

Our results show that reproduction of *T. merianae* from central Argentina is markedly seasonal, with both sexes concentrating their reproductive activities in October, November and December, demonstrating a synchronised reproductive cycle. Size at maturity was lower in males than females and the percentage of reproductive individuals was lower in females than males. The frequency of reproductive individuals was low in smaller body size classes in both sexes, being lower in females. In females, the proportion of reproductive individuals was different among body size classes, being over 50% in females larger than 39.5 cm SVL. This suggests that smaller females may not reproduce every year. Life history traits are determined by proximal responses to variation in environmental parameters (Stearns 1992). Environmental variability may be responsible for within-population variation. Andrade et al. (2004) showed that in south-eastern Brazil, by early September, T. merianae begin to emerge from dormancy and breeding takes place approximately one month after the tegus have emerged. By mid-October, females are gravid, with extended bellies, and egg

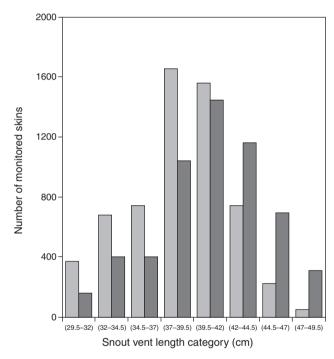


Fig. 5. Frequency distribution of estimated body size for females (grey) and males (black) *Tupinambis merianae* monitored during 2005–06 and 2006–07.

laying occurs (Lopes and Abe 1999). Cei (1993) shows that courtship and copulation occurs between October and November, and postures in November. The Espinal and Pampa regions have very different ambient climate and the resources may be different (Viglizzo *et al.* 1997; Brown *et al.* 2006; Cardozo *et al.* 2012). Bioclimatic and resource variability may be the cause of extension of the breeding season into December.

In relation to monitoring, width of dried skins was positively related to the size of live specimens. *Tupinambis merianae* is an oviparous species whose females store many eggs. Females had larger interlimb length and bigger abdominal perimeter (Cardozo *et al.* 2015); however, skin width did not differ between the sexes in estimating the size of the specimens. Skin width measurements provide an understanding of population structure from skin monitoring data. The national legislation

regulating the commercialisation and use of Tupinambis lizard is applied in all Argentine provinces where T. merianae and T. rufescens are present (Porini 2006). In addition to the national legislation, there is a current management plan for Tupinambis spp. that has the following features: (1) at a regional scale. restrictive measures are implemented - only skins of at least 24 cm wide can be sold; (2) indirect population monitoring, based on skin measurements at tanneries; and (3) a hunting season from December to March. Notably, this season is not enshrined in national law (Res. N° 11/2011 and Res. N° 1564/ 2013 Secretaría de Ambiente y Desarrollo Sustentable de la Nación Argentina) and these rules are based mainly on parameters from T. rufescens (Porini 2006). Despite similarities between the two species (Naretto et al. 2014) and their phylogenetic relatedness (Cabaña et al. 2014), they differ in reproductive parameters (Blengini et al. 2014). Fitzgerald et al. (1993) showed that gravid female T. rufescens from northern Argentina have an average SVL of 35.8 cm (minimum 33.0 cm SVL) and 78% of the females larger than 32 cm SVL had reproduced. Moreover, gonadogenesis peaked in November for females; testis mass peaked in November and decreased in December in T. rufescens. These biological parameters for T. rufescens differ from those observed for T. merianae, which showed larger sizes at maturity and different percentages of reproductive individuals. Lizards are known to show significant geographical variation in a wide range of life history traits across localities (Du et al. 2005; Shine et al. 1999). Hence, geographical variation in reproductive output is linked to geographical variation in adult body size, as it is for other reptile species (Fitch 1985). The Argentinian national legislation that regulates Tupinambis hunting does not provide for differences between species or areas (Res. Nº 11/2011 and Res. Nº 1564/2013 Secretaría de Ambiente y Desarrollo Sustentable de la Nación Argentina). The Tupinambis management plan in Argentina is well developed and has some strong aspects, but it must be adapted to local conditions regarding the species. Therefore, local studies are required to ensure regional differences can be included in the regulations. In some provinces, the legislation is more specific and establishes the hunting season and minimum size of the prey. In central Argentina, the breeding season coincides with hunting seasons allowed under national legislation. However, based on our studies, the closed season should include early December, to protect gravid females.

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Management of *Tupinambis* lizards includes policies aimed at influencing population growth rate by targeting large adult lizards and avoiding harvest of subadults (Porini 2006). Our results show that the width of dried skins reflects SVL of live individuals. Analysis of the harvest for the 2005–06 and 2006–07 seasons provides a picture of body sizes harvested, to determine a baseline for the harvested population. It reflects gender differences, showing that males are larger than females. Population structure based on skin size estimates is similar to that resulting from measurements of live specimens. The smaller size classes among captured lizards had a greater proportion of females than males. The minimum capture size permitted by national legislation (24 cm skin width) corresponds to live animals of 29.3 cm SVL. Reproductive parameters measured in our study for Córdoba populations suggest this

would allow capture of females that had never reproduced. We have suggested that the Córdoba wildlife agency increases the minimum sellable skin width. They increased the local limit to 27 cm, representing animals of 33.2 cm SVL to ensure that immature individuals are not captured. For dried skins 30 cm in width, the protected size classes are those with higher proportions of individuals with low reproduction rates; thus, we suggest gradually increasing the minimum size to this limit in order to enable these lizards to reproduce. Conservation management in lizards should focus on ways to protect subadults because the survival of young individuals and the proportion of smaller females that reproduce in a given year are both highly variable, and could affect the capacity of the population to regenerate (Dunham 1982; Fitzgerald 1994). Both size at sexual maturity and reproductive period should be taken into account to minimise the impact of harvesting on population recruitment. Finally, fecundity relationships indicate that larger females are more fecund, thus there should be a maximum size limit, to protect these individuals.

Management implications

Our study provides a cautionary tale about the dangers of extrapolating from related species when attempting to establish norms for harvesting wild populations. We recommend that management strategies consider each Tupinambis species differentially. Even though it may not provide a basis for quantitative estimates of offtake levels, knowledge of species biology may help to frame management plans that minimise the ecological impact of the trade (Shine et al. 1999) by identifying times when harvesting should not occur. December should not be included in the capture period for T. merianae in central Argentina. This kind of local and species-specific information is very important for management strategies. Plans may incorporate information on lizard biology from many specific localities. This kind of study is well suited to the resources available to government agencies. We offer an equation that can be used as a management tool for estimating the SVL of live *T. merianae* from their skins:

Snout-vent Length Estimate (cm) = (Skin Width (cm)
$$-1.007$$
)/0.78

Also, this equation allows us to suggest a minimum width of 30 cm for dried skins because this represents animals larger than 37 cm SVL. Continued work of this kind could provide data valuable for planning the long-term management of *Tupinambis* populations.

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References

- Andrade, D. V., and Abe, A. S. (1999). Gas exchange and ventilation during dormancy in the tegu lizard *Tupinambis merianae*. The Journal of Experimental Biology 202, 3677–3685.
- Andrade, D. V., Sanders, C., Milsom, W. K., and Abe, A. S. (2004).
 Overwintering in Tegu lizards. In 'Life in the Cold: Evolution, Mechanisms, Adaptation, and Application. Twelfth International Hibernation Symposium'. (Eds B. M. Barnes and H. V. Carey.)
 Biological Papers of the University of Alaska, No. 27. pp. 339–348. (Institute of Arctic Biology, University of Alaska: Fairbanks, AL.)
- Avila-Pires, T. C. (1995). Lizards of Brazilian Amazonia (Reptilia: Squamata). Zoologische Verhandelingen Leiden 299, 546–564.
- AVMA (American Veterinary Medical Association) (2013). Guidelines on euthanasia (formerly report of the AVMA panel on euthanasia). Available at http://www.avma.org/issues/animal_welfare/euthanasia.pdf [Verified January 2016]
- Blengini, C. S., Naretto, S., Cardozo, G., Giojalas, L. C., and Chiaraviglio, M. (2014). Variability in sperm form and function in the context of sperm competition risk in two *Tupinambis* lizards. *Ecology and Evolution* 4, 4080–4092. doi:10.1002/ece3.1262
- Böhm, M., Collen, B., Baillie, J. E. M., Bowles, P., Chanson, J., Cox, N., Hammerson, G., Hoffmann, M., Livingstone, S. R., Ram, M., Rhodin, A. G. J., Stuart, S. N., van Dijk, P. P., Young, B. E., Afuang, L. E., Aghasyan, A., García, A., Aguilar, C., Ajtic, R., Akarsu, F., Alencar, L. R. V., Allison, A., Ananjeva, N., Anderson, S., Andén, C., Ariano-Sánchez, D., Arredondo, J. C., Auliya, M., and Austin, C. C. (2013). The conservation status of the world's reptiles. *Biological Conservation* 157, 372–385. doi:10.1016/j.biocon.2012.07.015
- Brown, J. H., Stevens, G. C., and Kaufman, D. M. (1996). The geographic range: size, shape, boundaries and internal structure. *Annual Review of Ecology and Systematics* 27, 597–623. doi:10.1146/annurev.ecolsys. 27.1.597
- Brown, A., Martinez Ortiz, U., Acerbi, M., and Corcuera, J. (2006). 'La Situación Ambiental Argentina 2005'. (Fundación Vida Silvestre Argentina: Buenos Aires.)
- Cabaña, I., Gardenal, C. N., Chiaraviglio, M., and Rivera, P. C. (2014). Natural hybridization in lizards of the genus *Tupinambis* (Teiidae) in the southernmost contact zone of their distribution range. *Annales Zoologici Fennici* 51, 340–348. doi:10.5735/086.051.0306
- Cardozo, G., and Chiaraviglio, M. (2011). Phenotypic plasticity of life history traits in relation to reproductive strategies in *Boa constrictor* occidentalis. Evolutionary Ecology 25, 1163–1177. doi:10.1007/ s10682-011-9465-y
- Cardozo, G., Naretto, S., Zak, M., and Chiaraviglio, M. (2012). The role of landscape in contact zones of sister species of lizards. In 'Perspective on Nature Conservation Patterns, Pressures and Prospects'. (Ed. J. Tiefenbacher.) pp. 161–176. (Intech: Rijeka, Croatia.)
- Cardozo, G., Naretto, S., Blengini, C. S., and Chiaraviglio, M. (2015). Phenotypic diversity in female body shape is related to reproductive potential in *Tupinambis merianae* lizards. *Annales Zoologici Fennici* 52, 129–144.
- Cei, J. M. (1993). 'Reptiles del Noroeste, Nordeste y Este de la Argentina. Herpetofauna de las Selvas Subtropicales, Puna y Pampas.' (Museo Regionale di Scienze Naturali, Monografie XIV: Torino, Italy.) CITES. Appendix II. http://www.cites.org/esp/app/appendices.php [Verified December 2015]

- Cox, R. M., Skelly, S. L., and John-Alder, H. B. (2003). A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution* **57**, 1653–1669. doi:10.1111/j.0014-3820.2003.tb00371.x
- Díaz, J. A., Pérez-Tris, J., Bauwens, D., Pérez-Aranda, D., Carbonell, R., Santos, T., and Tellería, J. A. (2007). Reproductive performance of a lacertid lizard at the core and the periphery of the species' range. *Biological Journal of the Linnean Society. Linnean Society of London* 92, 87–96. doi:10.1111/j.1095-8312.2007.00877.x
- Du, W. G., Ji, X., Zhang, Y. P., Xu, X. F., and Shine, R. (2005). Identifying sources of variation in reproductive and lifehistory traits among five populations of a Chinese lizard (*Takydromus septentrionalis, Lacertiade*). *Biological Journal of the Linnean Society. Linnean Society of London* 85, 443–453. doi:10.1111/j.1095-8312.2005.00508.x
- Dunham, E. A. (1982). Demographic and life history variation among populations of the iguanid lizard *Urosaurus ornatus*: implications for the study of life-history phenomena in lizards. *Herpetologica* 38, 208–221.
- Fitch, H. S. (1970). Reproductive cycles of lizards and snakes. *Miscellaneous Publications of the Museum of Natural History University Kansas* **52**, 1–247.
- Fitch, H. S. (1985). Variation in clutch and litter size in New World reptiles. University of Kansas Museum of Natural History. Miscellaneous Publications 76, 1–76.
- Fitzgerald, L. A. (1994). The interplay between life history and environmental stochasticity: implications for management of exploited lizard populations. *American Zoologist* **34**, 371–381. doi:10.1093/icb/34.3.371
- Fitzgerald, L. A., Chani, J. M., and Donadio, O. E. (1991). *Tupinambis* lizards in Argentina: implementing management of a traditionally exploited resource. In 'Neotropical Wildlife: Use and Conservation' (Ed. J. Robinson and K. Redford.) pp. 303–316. (University of Chicago: Chicago, IL.)
- Fitzgerald, L. A., Cruz, F. B., and Perotti, G. (1993). The reproductive cycle and the size of maturity of *Tupinambis rufescens* (Sauria: Teiidae) in the Dry Chaco of Argentina. *Journal of Herpetology* 27, 70–78. doi:10.2307/1564908
- Garcia Valdez, M. V., Chamut, S., Valdez Jaen, G., Arce, O. E. A., and Manes, M. (2011). Dynamics of ovarian follicles in *Tupinambis merianae* lizards. *Acta Herpetologica* 6, 303–313.
- Getz, W. M., and Haight, R. G. (1989). 'Population Harvesting: Demographic Models of Fish, Forest and Animal Resources.' (Princeton University: NJ.)
- Gibbons, J. W., Scott, D. E., Ryan, T. J., Buhlmann, K. A., Tuberville, T. D., Metts, B. S., Greene, J. L., Mills, T., Leiden, Y., Poppy, S., and Winne, C. T. (2000). The global decline of reptiles, déjà vu amphibians. *Bioscience* 50, 653–666. doi:10.1641/0006-3568(2000)050[0653:TGD ORD]2.0.CO;2
- Kwiatkowski, M. A., and Sullivan, B. K. (2002). Mating system structure and population density in a polygynous lizard, *Sauromalus obesus* (=alter). Behavioral Ecology 13, 201–208. doi:10.1093/beheco/13.2.201
- Lanfri, S., Di Cola, V., Naretto, S., Chiaraviglio, M., and Cardozo, G. (2013).
 Understanding the ecological niche to elucidate spatial strategies of the southernmost *Tupinambis* lizards. *Amphibia-Reptilia* 34, 551–565. doi:10.1163/15685381-00002917
- Lopes, H. R., and Abe, A. S. (1999). Biologia reprodutivo e comportamento do teiú, Tupinambis merianae, em cativeiro (Reptilia, Teiidae). In 'Manejo y Conservación de Fauna Silvestre en América Latina'. (Eds T. G. Fang, O. L. Montenegro and R. E. Bodmer.) pp. 259–272. (Instituto de Ecología: La Paz, Bolivia.)
- Madsen, T., Ujvari, B., Shine, R., and Olsson, M. (2006). Rain, rats and phytons: climate driven population dynamics of predators and prey in tropical Australia. *Austral Ecology* **31**, 30–37. doi:10.1111/j.1442-9993. 2006.01540.x

Mercolli, C., and Yanosky, A. A. (1990). Repertoire des comportements du Teju (*Tupinambis teguixin*). Sauria: Teiidae. Revue francaise d'Aquariology et Herpetologie 16, 123–130.

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- Mieres, M. M., and Fitzgerald, L. A. (2006). Monitoring and managing the harvest of Tegu Lizards in Paraguay. The Journal of Wildlife Management 70, 1723–1734. doi:10.2193/0022-541X(2006)70[1723: MAMTHO12.0.CO:2
- Naretto, S., Cardozo, G., Blengini, C. S., and Chiaraviglio, M. (2014). Sexual selection and dynamics of jaw muscle in *Tupinambis* lizards. *Evolutionary Biology* 41, 192–200. doi:10.1007/s11692-013-9257-0
- Nobrega Alves, R. R., and Pereira Filho, G. A. (2007). Commercialization and use of snakes in North and Northeastern Brazil: implications for conservation and management. *Biological Conservation* 16, 969–985.
- Norman, D. R. (1987). Man and tegu lizards in eastern Paraguay. *Biological Conservation* 41, 39–56. doi:10.1016/0006-3207(87)90046-2
- Porini, G. M. (2006). Proyecto *Tupinambis*, una propuesta para el manejo de *Tupinambis rufescens* y *T. merianae* en la Argentina. In 'Manejo de Fauna Silvestre en la Argentina. Programas de uso sustentable'. (Ed. M. L. Bolkovic and D. Ramadori.) pp. 65–75. (Dirección de Fauna Silvestre, Secretaría de Ambiente y Desarrollo Sustentable: Buenos Aires.)
- Rodda, G. H., McCoid, M. J., Thomas, T. H., and Campbell, E. W. (1999).
 Population trends and limiting factors in *Boiga irregularis*. In 'Problem Snake Management: the Habu and the Brown Treesnake'. (Eds G. H. Rodda, Y. Sawai, D. Chiszar and H. Tanaka.) pp. 236–253. (Cornell University Press: Ithaca, NY.)
- Rodda, G. H., Campbell, E. W., and Thomas, T. H. (2001). A high validity census technique for herpetofaunal assemblages. *Herpetological Review* 32, 24–30.
- Rohr, D. H. (1997). Demographic and life-history variation in two proximate populations of viviparous shrink separated by a steep altitudinal. *Journal of Animal Ecology* 66, 567–578. doi:10.2307/5950
- Shine, R., Harlow, P. S., Keogh, J. S., and Boeadi. (1996). Commercial harvesting of giant lizards: the biology of water monitors (*Varanus salvator*) in southern Sumatra. *Biological Conservation* 77, 125–134. doi:10.1016/0006-3207(96)00008-0

- Shine, R., Ambariyanto, Harlow, P. S., and Mumpuni. (1998). Ecological traits of commercially harvested water monitors, *Varanus salvator*, in northern Sumatra. *Wildlife Research* 25, 437–447. doi:10.1071/ WR97118
- Shine, R., Ambariyanto, Harlow, P. S., and Mumpuni. (1999). Reticulated pythons in Sumatra: biology, harvesting and sustainability. *Biological Conservation* 87, 349–357. doi:10.1016/S0006-3207(98)00068-8
- Stearns, S. C. (1992). 'The Evolution of Life Histories.' (Oxford University Press: Oxford, UK.)
- Vaira, M., Akmentins, M., Attademo, M., Baldo, D., Barraso, D., Barrionuevo, S., Basso, N., Blotto, B., Cairo, S., Cajade, R., Céspedez, J., Corbalán, V., Chilote, P., Dúre, M., Falcione, C., Ferraro, D., Gutierrez, F. R., Ingaramo, M. R., Junges, C., Lajmanovich, R., Lescano, J. N., Marangoni, F., Martinazzo, L., Marti, R., Moreno, L., Natale, G. S., Perez Iglesias, J. M., Peltzer, P., Quiroga, L., Rosset, S., Sanabria, E., Sanchez, L., Schaefer, E., Ubeda, C., and Zaracho, V. (2012). Categorización del estado de conservación de los anfibios de la República Argentina. Cuadernos de Hervetología 26. 131–159.
- Viglizzo, E., Roberto, Z., Lértora, F., and López Gay, E. (1997). Climate and land-use change in field-crop ecosystems of the Argentine Pampas. *Agriculture, Ecosystems & Environment* 66, 61–70. doi:10.1016/S0167-8809(97)00079-0
- Wapstra, E., Swain, R., and O'Reilly, J. M. (2001). Geographic variation in age and size at maturity in a small Australian viviparous skink. *Copeia* 2001, 646–655. doi:10.1643/0045-8511(2001)001[0646:GVIAAS]2.0. CO:2
- Webb, J., Brook, B. W., and Shine, R. (2002). What makes species vulnerable to extinction? Comparative life-history traits of two sympatric snakes. *Ecological Research* 17, 59–67. doi:10.1046/j.1440-1703.2002.00463.x
- Zak, M., and Cabido, M. (2008). What drives accelerated land cover change in central Argentina? Synergistic consequences of climatic, socioeconomic, and technological factors. *Environmental Management* 42, 181–189. doi:10.1007/s00267-008-9101-y
- Zak, M. R., Cabido, M., and Hodgson, J. (2004). Do subtropical seasonal forests in the Gran Chaco, Argentina, have a future? *Biological Conservation* 120, 589–598. doi:10.1016/j.biocon.2004.03.034